

the staminate inflorescence is usually unbranched, the flowers bear six to eight greenish petals, and other parts are in fives or eights.

The two species share a similar ecology. They are often found as large isolated trees, usually in wet places on old alluvium. Saplings form dense stands along broken streams and gaps achieving a short-lived dominance of the understory. Nothing much is known about pollination and dispersal.

These are the fastest growing trees of Asia and should be planted more often in reclamation and reforestation schemes where the ground is wet and a quick shade is required. More study is needed on the insect pests that so consistently nibble the leaves.

**OCTOMELES.** [Greek in reference to the eight-parted flowers.] Monotypic, *Octomeles sumatrana*, generally as *binuang* in Malay. It is found in Sumatra and throughout Borneo then north in the Philippine Islands as far as northeastern Luzon, and east to the Solomon Islands and New Guinea. It is perhaps less inclined to the

very strong dry seasonal lands, with suggestions sometimes made that the tree is only weakly deciduous.

**TETrameLES.** [Greek in reference to the four-parted flowers] Monotypic, *Tetrameles nudiflora*, an abundant and consistent element of the early successional lands in mainland Asia from north India at 1000 m elevation, south to Sri Lanka, east to all of Indochina and south into the northernmost Malay Peninsula, then disjunct to the Lesser Sunda Islands, easternmost Borneo, Sulawesi, east to New Guinea and discovered in 1972 on the Cape York Peninsula of Australia.

The papery simple leaves are alternate and clustered at the twig tips with a more or less cordate base, 12-18 cm wide. Male inflorescence is spikes in fascicle, 5-7 cm long. Male flowers numerous, minute. Sepals four; petals one-four or none. Female inflorescence spike-like, terminal, 20 cm long. Female flowers sessile. Sepals connate into a tube with four small lobes. Fruit a small capsule

A deciduous tree, usually bare preceding the dry months of December to February. Seedlings are recruited in full sun of wet gaps or stream beds.

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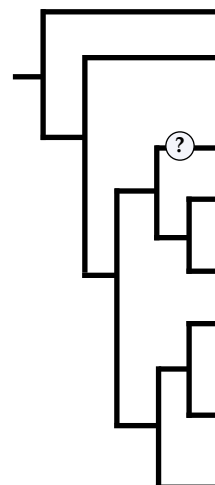
FAGALES

This wonderful order includes the oaks, beeches and birches, hickories and walnuts, trees that are widespread and abundant in the high latitudes, and trees whose tim-

ber, resins, bark, nuts and acorns fuel both the human economy and the natural ecology of the north. From such a northern view you might characterize the order as comprising tanniniferous and deciduous trees with simple pinnately nerved or pinnately compound leaves,

<sup>1</sup>Li, R. *et al.* 2004. International Journal of Plant Science 165: 311–324.

Phylogeny of Fagales

	Family	Diversity & Distribution	Trees of Tropical Asia
	Nothofagaceae	1/35, New Guinea to South America.	0
	Fagaceae	10/670, more or less worldwide (not tropical Africa or Australia, poor in tropical S America); simple, stipulate, pinnate nerved, toothed.	7/250, especially montane, but also rich and abundant in everwet lowlands, poor in seasonally dry lowlands.
	Myricaceae	3/57, Cosmopolitan except Australia, glan-dular aromatic,	1/3, especially littoral, exposed summits.
	Juglandaceae	7/50, North temperate to Argentina and Sundaic Region of Asia; spiral pinnate com-pound, without stipules, leaflets serrate.	1/5-9, widely in the region, with 4 other genera near the Chinese border.
	Rhoipteleaceae	1/1, <i>R. chiliantha</i> , China reaching Vietnam, compound pinnate.	0
	Ticodendraceae	1/1, <i>T. incognitum</i> , Central America; doubly-serrate leaves that have stipules encircling the stem, carpels with two long stigmas.	0
	Betulaceae	6/145 North Temperate to Andes ; de-ciduous; stipulate, doubly serrate leaves, catkinate inflorescences.	3/6, not east of montane Mainland SE Asia.
	Casuarinaceae	1 (or 4)/95. tropical Asia to SW Pa-cific, especially Australia; photosynthetic branchlets, full sun, nitrogen fixing via actinomyce.	1/4, <i>C. equisetifolia</i> littoral, others in mountains.

with toothed margins (nerves irrigating the non-glandular teeth), mycorrhizal, some with *Frankia* infection via root hairs, monoecious, small flowers in a spike or catkin, wind-pollinated and heavy fruited. In such a description you would not be wrong, but you would be overlooking the insect pollinated Asian tropical oaks, the southern beeches of *Nothofagus*, the enigmatic and switchy *Casuarina* and the half-hidden tropical trees of *Engelhardtia*. The story of the Fagales spanning the last

80 million years would tell us much of how the forests of the world came to be, and such a story must include as a main theme the Fagales of tropical Asia.

The order includes eight families, 55 genera and about 2000 species. The Fagales are strongly monophyletic although their relative position within tricolpates remains unsettled. *Myrica* holds the most equivocal position. The drawn phylogeny follows the cited study and STEVENS *loc. cit.*

## #

### ROSIDS (FABIDS): FAGALES

#### FAGACEAE

**NAME:** From the genus *Fagus*, the classical name for the European beech. Sometimes as the oak family, but it also includes the beeches and chestnuts. Common names in Asia apply somewhat variably to groups, with supplemental adjectives for individual species: for silvery-blue lower leaves and acorns (*Lithocarpus* and *Quercus*) the Malay is *empenit* or *mempening*, Tagalog is *pangnan*; for leaves coppery below and spiny fruit (*Castanopsis*) the Malay is *berangan*, Tagalog *talakatak*. The many different languages spoken in the mountains have widely varying names, but most distinguish acorns and chestnuts.

**OVERVIEW:** A family of 10 genera and maybe 670 species although the exact species richness is uncertain (between 600-1000) owing to uncertain limits of hybridization and the similarity of vegetative form among many species. Fagaceae are more or less worldwide in distribution but absent from tropical and Southern Africa, while the American distribution is somewhat complex in that the family is abundant to dominant in the Northern latitudes, claims more than a dozen species in the Meso-American mountains where it is sometimes dominant at 1200-2000 m, although rarely in the lowlands, and nearly absent from South America where it is found in the higher mountains by a single species of *Quercus* and a species of *Columbobalanus*. By contrast, the family is both species-rich and abundant in the lowland equatorial forests of Asia, and even more so at altitudes of 1000 m. Mt. Kinabalu in Borneo holds a special place of honor in Fagaceae diversity with four genera and 62 species (12 *Castanopsis*, 38 *Lithocarpus*, 11 *Quercus* and the monotypic *Trigonobalanus*). Compare such numbers with the 97 species usually credited for all of North America. The family is also abundant and diverse in the dry-seasonal tropics of mainland Asia although increasingly restricted to the uplands as we move from northern Malaya to Thailand and Indochina. (The family representatives of Northern Thailand are extensively illustrated in GARDNER *loc. cit.*) The family declines toward Wallace's line and is sparse or absent from most of the Lesser Sunda Islands and poor or absent alto-

gether eastward where *Nothofagus* (Nothofagaceae) appears in its place. The following table makes two further points regarding distribution. The three principle genera are relatively species-rich in the Philippine, the Sundaic Region and in Mainland SE Asia, but most species are narrowly distributed.

#### FIELD RECOGNITION: FAGACEAE

Small and medium canopy trees, sometimes large diameters, but not tall (often with suckers and sprouts around the base, the leaves on the sprouts differ from the mature leaf).

Bark falls easily from the wood, the rays are wide and appear as slits entering the wood (*Lithocarpus* and *Quercus*) or the rays are narrow; and uniform *Castanopsis*).

Resins or tannins, but with only scant clear watery exudate;

Vegetative buds scaly, often a thickened pair of terminal buds, twigs terete or angled, often pronounced lenticels

Leaves spirally arranged, sometimes clustered or nearly whorled (*Quercus*) or most often in a flat plane (*Lithocarpus* and *Castanopsis*)

Stipules always present, but early deciduous, sometimes small, but at least a minute scar present

The leaf stalk typically with a swollen base, slender as it joins the blade which often extends down the stalk slightly

The nerves generally strong, arched and regular, some arching to the margin, some strongly looped, in *Quercus* the main nerves emerge from the margin as teeth;

The blade is usually silver or metallic blue sheen below (*Lithocarpus*) or green or copper (*Castanopsis*).

Domatia are fairly common, represented by hair tufts.

Species are most easily identified by reference to their acorns, often found beneath the tree. Even rotted acorns can be useful.

#### FIELD CONFUSION

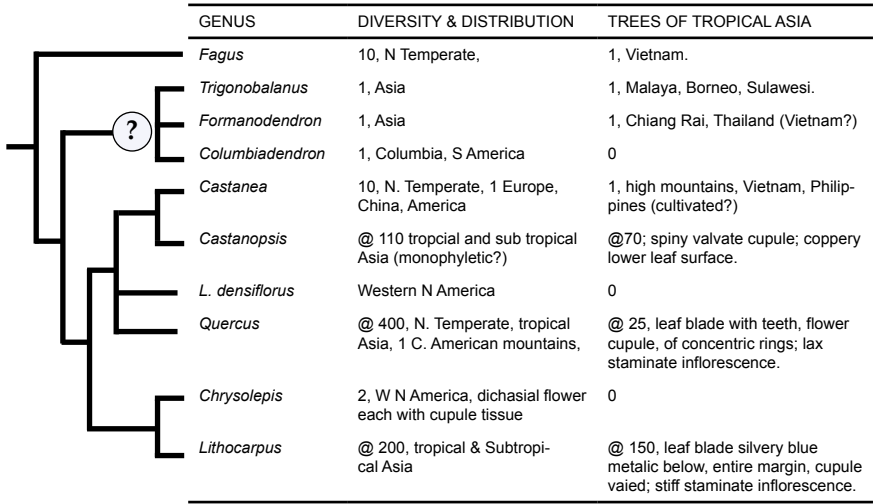
Sapotaceae because of the swollen lower stalk, and clustered stipules, but these bear white exudate and an entirely different bark.

In *Shorea* and other mountain Dipterocarpaceae the nerves may be similar while the small stipule and resinous aspect create a similar appearance, but the leaf stalk is swollen at the upper end, and the fine venation is scalariform.

Some Lauraceae, because of the absence of exudate, and again because of the swollen lower portion of the stalk; and some have the shiny metallic lower surface of the oaks and some *Actinodaphne* bear scale leaves that can give the appearance of an oak with clustered leaves (vs. *Quercus*, look for trace of teeth!). However the bark and wood in laurels is usually crumbly, and the odor is often sweet aromatic resinous.

Phylogeny of Fagaceae

Clades within the Fagaceae following Manos, Zhou & Cannon<sup>2</sup>. The beech (*Fagus*) is basal, the three 'trig-oaks' may be monophyletic, but some details of form and fossil raise doubts<sup>2</sup>; the chestnuts (*Castanea* and *Castanopsis*) and oaks (*Quercus*) appear as sister taxa; the Asian stone oaks (*Lithocarpus*) are strongly monophyletic, while the one species of Western North America formerly in *Lithocarpus* (*L. densiflorus*) needs to be transferred.



The Fagaceae are characterized by a densely tanniniferous body supported by ectotrophic mycorrhiza. The leaves are simple, pinnately veined and stipulate or at least with obvious stipule scars. The twigs are usually lenticellate and variously angled and ridged.

The flowers of Fagaceae are small, often less than two mm across, unisexual-monoeocious, with parts in threes, the perianth reduced in size in one or two series, the anthers four to 20. A wealth of literature concerns just how the cupule that surrounds the mature ovary develops because it appears to be far from uniform. The current

consensus is that the cupule develops from sterile branches of the inflorescence in one of two ways. The first type is called a flower cupule in which a single pistillate flower is surrounded by a cupule that derives from tissue at the flower base. This type is restricted to most species of *Lithocarpus*. The contrasting type is called a dichasium cupule in which one or more pistillate flowers are surrounded by modified axes from the subtending inflorescence. In this fashion, fruit of the dichasial type, such as the chestnuts, bear several seeds in a cupule that is strongly valved and breaks apart at maturity. While the two types are very different, close similarity in final form can arise when the number of flowers is reduced to one. Thus, some argue that the acorn of *Quercus*, in contrast to *Lithocarpus*, is a single fruit surrounded by a branch complex.

The tropical oaks and chestnuts may well be the most ecologically neglected plant family in Asia. Some notes on their ecology are in order if only to encourage further investigation; these notes apply equally to all of the component genera.

Our knowledge of pollination in tropical Fagaceae is weak. Certainly, we know that while the oaks and chestnuts of north latitudes are exclusively wind-pollinated, their tropical relatives do not behave the same way. The clouds of insects attracted to the dense and odorous floral displays attest to the prevalence of insect pollination. It is commonly said that the tropical species of *Quercus*, which bear pendent inflorescences, are wind-pollinated while those with upright inflorescences, especially *Lithocarpus*, are insect pollinated. To see *Quercus lineata* in Northern Thailand, leafless on a sunlit hillside, and

Genus	D. Sutep	shared	Malaya	shared	Philipp.
Castanopsis	7	1	17	0	5
Quercus	11	0	8	0	2
Lithocarpus	12	1	25	2	21

The table below shows the number of species of Fagaceae genera in three locations: Doi Sutep National Park Thailand<sup>1</sup> (only 25,000 ha area), Peninsular Malaysia (following the On-Line Checklist); and the Philippines following Leonardo L. Co's unpublished update of MERRILL. The intervening columns show the number of species shared between adjacent regions. (No species are shared between north Thailand and the Philippines.)

<sup>1</sup>Maxwell, J. et al. 2001. Vegetation and vascular flora of Doi Sutep-Pui National Park, Northern Thailand. Thai Studies in Biodiversity No. 5: 1-205.

<sup>2</sup>Manos, P. et al. 2001. International Journal of Plant Science. 162: 1361-1379.

dense with pendent catkins, it is easy to conclude that the tree is wind pollinated in the manner of its northern congeners. But what of *Quercus argentata*, an evergreen species of the mid canopy in the everwet and humid forests of the Malay Peninsula? Here we find a decisive conflict between two long-held dogma: (1) that wind is an ineffective agent of pollination anywhere in the wet equatorial forests; (2) that insect pollination is ancestral to wind, and that reversals from wind to insect pollination never occur. Are we wrong about the efficacy of wind pollination in the wet forests? If not, and if *Quercus argentata* and other lowland equatorial species are insect pollinated, does that represent an ancestral condition in the genus? A further critical question regards how pollination changes as we move from the lowlands of the Malay Peninsula to the dry-seasonal mountains in Thailand and then northward to southern China. At what point does wind pollination become dominant, and does the transition ever involve the same or related species?

Dispersal of the bulky seeds of acorns and chestnuts also remains a mystery. The common and reasonable assumption is that they are taken and scatter-hoarded by small mammals. Certainly a great many acorns are destroyed by arboreal mammals before they ever fall and tropical deer and pigs relish them as much as do their northern cousins. With respect to dispersal, the relative poverty of the family in the Cordillera of Luzon Island, Philippines is interesting and in contrast to the richness found in Borneo to the south or in Taiwan to the north. The low richness in Luzon is coincidental (or related?) with the absence of squirrels in the same area. Nine species of squirrels are known for the Philippines but these are restricted to the south with two from Mindanao and six from Palawan and only one as far north as Mindoro and Leyte, but none in northern Luzon. Perhaps cloud rats are ecologically similar in the Cordillera.

Although CORNER *loc. cit.*, says that *Quercus pseudo-verticillata* is completely deciduous in northern Malaya, the majority of the equatorial species are certainly evergreen with a seasonal phenology of leaf flush and growth. Some of the ruderal *Lithocarpus* seem to be in flower and fruit frequently. However, most species display supra-annual variation in at least flower and fruit volume and evidently mast in five and ten year cycles.

In the oaks we find a rich association with mycorrhiza, especially the gill fungi and Polypore basidiomycetes, the sporocarps of which are so conspicuous at certain times of the year. The role of mycorrhiza may well be the most critical of ecological issues in the family, an issue that is perhaps paralleled in the Dipterocarpaceae. In this way, fungi may also be involved in the broader question of why the American equatorial lowland forests lack abundant dipterocarps and Fagaceae.

Parallels between the Dipterocarps and the Fagaceae are also seen in growth rates. When we look at 20 years of change at the 50-ha plot at Pasoh, Malaya and restrict our attention to those individuals of forest species that grew more than one cm per year, we find the species list dominated by, on the one hand, a half dozen species of red *merantis* (*Shorea* sect. *Mutica*) and on the other hand,

the Fagaceae, including *Quercus argentata*, *Castanopsis schefferiana* and *Lithocarpus rassa*.

Oak trees and human history are deeply intertwined, especially so in Europe, North America, China and Japan. The English oak, *Quercus robur*, provides ornament, shade, timber, forage and acorns for pigs, and bark for tanning leather. So it is a surprise that the economic exploitation of tropical oaks should be so paltry. The wood of our tropical oaks retains a reputation for low quality. Among *Lithocarpus*, the tannin content is often low and the wood susceptible to fungi and termites. It typically has wide rays that split the timber if it is not quartered and dried carefully. Many species are regarded as 'too hard' such that they shatter and split with nailing.

Galls are another historically important economic product of oaks. A gall forms when a wasp of the genus *Cynips* lays an egg in the vegetative bud. The gall becomes exceedingly rich in tannins, and these galls have been a valuable medicinal product for centuries. The classic galls are from *Q. infectoria* from Alepo Italy, carried by Arab traders to the East and on to China as early as the Tang Dynasty. These same European galls were likewise known in the ancient Malay world, called *majakani* and used in traditional medicine. It seems surprising that none of the local Fagaceae galls are so employed.

A few of the tropical chestnuts are considered edible, and at least a few are palatable. On the other hand, acorns, which were a staple food of Native Americans are evidently never eaten in Asia.

**FAGUS.** [Classical name of European beech.] The genus *Fagus* is sister to rest of Fagaceae. It comprises 10 species of the Northern Hemisphere, one of which *F. longipetiolata*, reaches south as far as from the higher mountains of northern Vietnam. It might yet be found in the second highest peak in Vietnam, the poorly explored Mount Ngoc Linh (2598 m) of the Central Highlands. (Not illustrated.)

**TRIGONOBALANUS.** [Greek, three-sided acorn.] A single species, *Trigonobalanus verticillata* with leaves in whorls, known from seven mountain sites in Malaya including Fraser's Hill, in Borneo on Kinabalu, and in Sumatra and Sulawesi. One would expect to find it in Mt. Apo, Mindanao as well. Although a rare and strange tree, it is abundant where it occurs. As the specific epithet suggests, *Trigonobalanus* is unusual in bearing toothed *Quercus*-looking stipulate leaves in tight spirals of three. It bears numerous small seeds that, unlike the acorns and chestnuts, germinate with the cotyledons above ground. Photographs of the tree and a reprint of E. J. Corner's discussion of its biology can be found in WONG & PHILLIPPS *loc. cit.* The genus is sometimes broadened to include *Formanodendron* from Yunnan and N. Thailand and *Columbobalanus* from NW South America<sup>3</sup>.

<sup>3</sup>Nixon, K. *et al.* 1989. American Journal of Botany 6: 828–841.

# Castanopsis



*Castanopsis*. 1-3, *C. megacarpum*, 100 m elevation, Pasoh Forest, Malaysia; 1, spiny fruit with unusually large seed, they fall to the ground where they are moved or eaten, especially by pigs; 2, rough bark, fresh leaves large and copper below; 3, new leaves flush red; 4-6, an unidentified *Castanopsis*, 2000 m, Central Highlands of Vietnam; 4, trunk with low buttresses (bark of photo 5 cut away); 5, inside of bark showing the wide rays that penetrate the bark; 6, the spiny small seeded fruit, at same scale as the bark; 7, some species of *Castanopsis* have a beery green lower surface, here with small fruit; 8, *C. oligoneura*, from the lowlands of Sarawak.

**FORMANODENDRON.** [Commemorates L. Forman, who described the genus *Trigonobalanus*.] Cupules splitting into three-five valves; nuts angular, winged five. *Formanodendron doichangensis*, from four

sites in southwest Yunnan, and from Chiang-Rai, northern Thailand, and is expected in the highlands of Vietnam.



**CASTANEA.** [Classical name of European chestnut.] Leaves deciduous; ovary six(-nine)-loculed. We find the widely cultivated Chinese chestnut, *Castanea mollissima*, occurring naturally in southern Yunnan, northern Vietnam and a single collection from 6000 feet in Benguet in Luzon, Philippines, debatedly native.

**CASTANOPSIS.** [Greek, resembling *Castanea*.] A genus of about 110 species of tropica Asia, 34 species treated in *Flora Malesiana*, 21 in Borneo. The stigmas is small and pointed, the male inflorescence stiff and the male flowers usually with a pistillode; stamens 12, anthers minute. Each cupule subtends a cluster of female flowers (sometimes reduced to one flower) divided into lobes or marked by vertical zones at least when young. The mature cupule is usually spiny and completely covering the fruit. Most species have a coppery lower leaf surface. Species vary in the size of the leaves and in the indumentum, the size of the fruit and the extent of spines. Some species are entirely spineless and the fruit can look like those species of *Lithocarpus* with enclosed acorns; these include *C. inermis* of Malaya and *C. fissa* of S China to Vietnam. The latter bears strongly toothed leaves and is illustrated in THROWER *loc. cit.* When spines are lacking, you often find that the wall breaks irregularly to display several fruits within.

**QUERCUS.** [Classical name for European oaks.] Perhaps 400 or more species, monophyletic, all species share unisexual inflorescences, a single pistillate flower subtended by a valveless cupule, and lax staminate inflo-

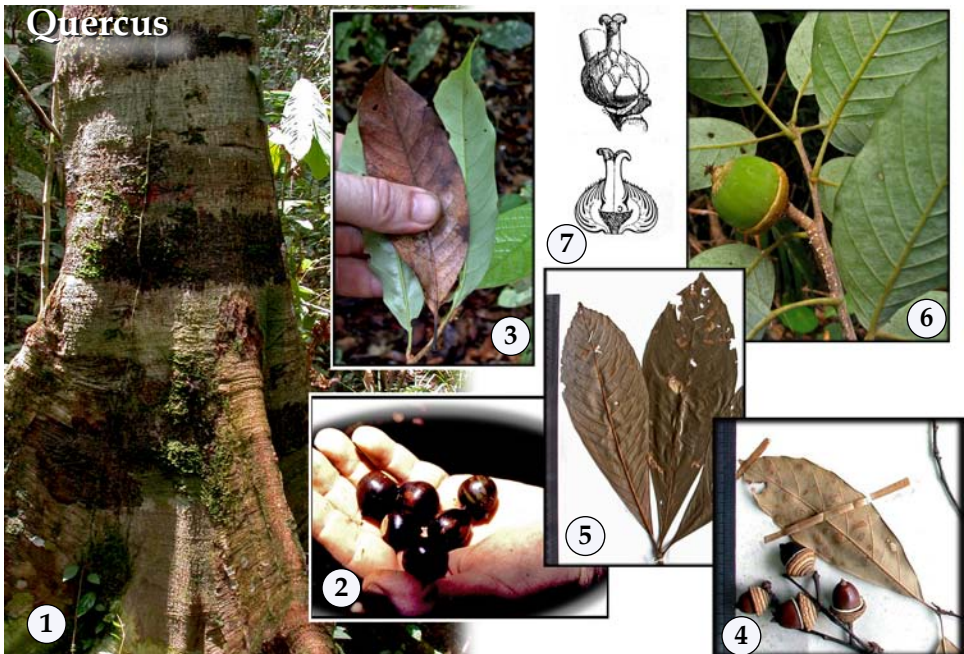
rescence (presumed wind-pollinated). The Asian tropical species appear to all belong to a distinct clade within *Quercus* representing subgenus *Cyclobalanopsis*.

The leaf blade of most of the tropical members of *Quercus* have at least a few marginal teeth, at least in the upper third of the leaf, and so differ from the always entire leaf margin of *Lithocarpus* and most equatorial species of *Castanopsis*. The acorns can usually be distinguished from the other genera because the warts of the cap are in concentric rings, not spiral. In places, the most abundant tree species in hill forests will be a *Quercus*, such as in *Q. oideocarpa* in Fraser's Hill, Malaya.

**LITHOCARPUS.** [Greek, stone fruit.] The Kew Checklist give 590 basionyms with 334 accepted species, but a number closer 200 is more likely. *Flora Malesiana* lists 110 species within its area. Once the single species attributed to western North America is removed, *Lithocarpus* is strongly monophyletic and exclusively tropical and subtropical Asian. They are distinguished by a non-valvate flower cupule subtending a single pistillate flower. Molecular data indicates two main constituent clades: one widespread across the entire range of the genus, and a second clade restricted to Borneo<sup>4</sup>.

Species almost always have a blue silver metallic sheen to the lower surface. The acorns vary in size and shape and especially in the extent to which the fruit is covered by the cupule. Be certain to see WONG & PHILLIPPS *loc. cit* for the photograph of *Lithocarpus revolutus* at Kinabalu with acorns as large as oranges.

<sup>4</sup>Cannon, C. *et al.* 2003. Journal of Biogeography. 30: 211–226.



*Quercus*. 1–2 *Q. argentata*; 1, tree 47 cm DBH, bark form and low stout buttresses; 2, acorns, 3–5, *Q. gemelliflora*; 3, fresh and fallen leaves, teeth; 4, herbarium specimen, acorns; 5, herbarium specimen of juvenile leaf, large, whorled, teeth; 6, *Quercus subsericea*, newly recorded from the Philippines, leaf stalk, lenticels, teeth, acorn. (Photograph 6 © Leonardo L. Co; 7, after BAILLON *loc. cit.*)



*Lithocarpus*. The names of individual species are in the photo documentation index; determination of *Lithocarpus* species usually requires mature acorns and good sample of twigs and leaves. 1, characteristic habit of *Lithocarpus* in flower, dense crown filled with fertile staminate spikes; note the mature acorns on the lower branches; 2-3, the twig is also warty lenticellate, the leaf stalk is slightly or greatly thickened where it joins the twig; 3, the lower leaf surface is blue and silvery with a metallic sheen; 4, mature tree is often broad but short, with warty gray lenticellate bark; 5, leaves can sometimes be nearly glaucous, the floral spikes are typically dense with small pale flowers; 6-9, the cupped acorn is characteristic but varies in all details; sometimes spiny, and sometimes completely encloses the fruit, but typically as in 9.



# MYRICACEAE

NAME: From the genus *Myrica*, now restricted to species of N America.

OVERVIEW: An small family formerly of three genera, the monotypic, *Canacomyrica monticola* of New Caledonia, and the monotypic *Comptonia peregrina* of N America. *Myrica* was for a long time treated as the third genus, comprising about 50 species, cosmopolitan in distribution except Australia. A comparison of molecular data for the the genus and for the actinomycetes that fix nitrogen within the root nodules showed that the two deciduous N American species are closer to *Comptonia* than to the evergreen tropical species and so the latter are now placed in the resurrected *Morella*<sup>1</sup>. The family remains ambiguously placed in the order.

MORELLA. [Uncertain, possibly a dimutive of *Morus*, the mulberry.] 40 species, cosmopolitan except Mediterranean and Australia. These shrubs are particularly common on sand near ocean shores and other utri-

ent poor soils including ultrabasics, exposed mountain tops and degraded lands. Patchily abundant but in general poorly represented in Asia, except for a few littoral species. All are small multi-branched shrubs, characterized by their strong resinous odor and strong nitrogen fixing actuated through root nodules bearing the actinomycete *Frankia*. They often come to dominance in degraded areas where little else can gain a foothold. The flowers are unisexual but the distribution of the sexes among spikes and trees appears to be more than a little plastic and when near-dioecy is found, sex-switching between years also occurs. The fruit is probably eaten by birds in those species which are fleshy. Among the littoral species, dispersal by seawater is presumed.

*Morella esculenta*, with entire leaf blade at maturity (pinnately invaginated in juvenile), the lower surface densely hairy; yellow gland-dotted and aromatic. It is especially widespread, on open coastal scrub in Singapore and also exposed montane slopes at 1000 m in Mainland SE Asia. *Morella javanica* the leaf blade wavy and with teeth, the lower surface smooth, hairless. Can be a tree to 30 m tall at 1500 m elev, but dwarfs at higher elevations, growing as a small prostrate sub-shrub near summits. edible fruit, planted for erosion control.

Given the extent of degraded land in tropical Asia today, a warning is in order regarding the invasive abilities of these plants. *Morella faya* was introduced to Hawaii and has naturalized and spread widely in the islands.

<sup>1</sup>Huguet, V. et al. 2005. Molecular Phylogenetics and Evolution. 34: 557-568.



*Morella esculenta*. Photographs from Singapore, seedling, habit and fruit; line tracing of *M. javanica*, from an upland site in Thailand. (Photographs © Joseph Lai.)



## ROSIDS (FABIDS): FAGALES

## JUGLANDACEAE

**NAME:** The family name is from the genus *Juglans*, derived from Latin, *Jupiter's-fruit*. The English common name *walnut* is sometimes applied to the family. That name itself is ancient, meaning 'foreign nut' in reference to the fact that the English walnut was introduced from Europe.

**OVERVIEW:** With seven genera and 50 species, the Juglandaceae are chiefly represented in E North American and E Asian, with minor representation in Europe, the Americas, and the tropics with *Alseodaphne* and *Juglans* in the south in temperate America, and with a very minor representation in tropical Asia. Juglandaceae are strongly monophyletic and distinguished within the Fagales by the pinnately compound spirally arranged leaves lacking stipules, often serrate margins, the blade with small, aromatic glands, and the inflorescences a spike of single, axillary flowers. Juglandaceae are among the more important trees of the North Temperate forests, providing timber and the cultivated walnut of commerce. Several genera reach the northernmost mountains of Vietnam and Laos where you find *Carya tonkinensis*, *Annamocarya sinensis*, *Platycarya strobilacea* and *Pterocarya*

(illustrated in THROWER *loc. cit.*), but they are not further treated here. For a global overview of the family see the on-line treatment for the *Flora of China* and especially the family and generic synopsis by Donald Stone<sup>2</sup>.

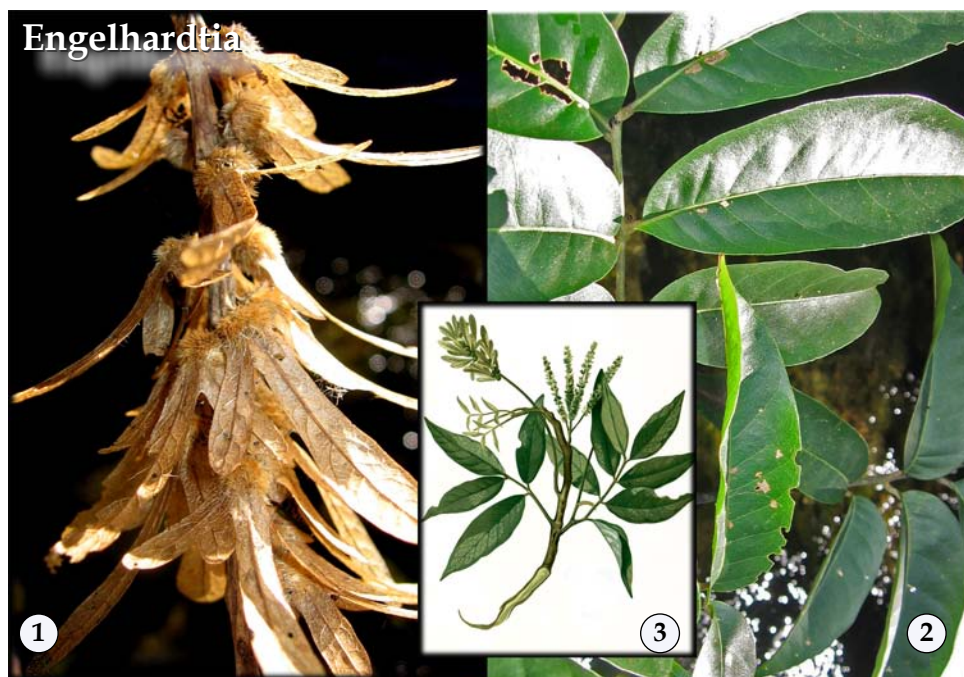
**ENGELHARDTIA.** [Commemorates N. Engelhardt, d. 1831, Dutch governor of Java.] The genus name by Blume was originally spelled in error as *Engelhardtia*, without the letter 't'. Some authors still follow that error.

These are strange and wonderful trees about which no one knows very much. A few individuals are found in almost every forest from China to Borneo and north to the Philippines, and cultivated in southern Japan. They occur both in the lowlands and in the mountains beyond 1000 m elevation. They are easily overlooked or ignored by professional botanist and native resident alike. Local names include the Iban *sangsanglang* and the Malay *momom*, but the trees are rarely recognized. Sterile specimens are often lost in 'unidentified Sapindaceae', especially if the margin of the leaflet lacks teeth. The typical dry leaf is a bicolored black-brown much like *Guioa* (Sapindaceae). Most often the leaflet has an asymmetric base, and the leaflets tend to increase in length from rachis base to apex. The leaf lacks a terminal leaflet, the margin is variably toothed, sparsely hairy or glandular in juveniles.

Although the genus is not well known, the story of *Engelhardtia* may well be central to the advent and spread of the entire walnut family. The closest relatives live in Central and South America under the two generic names, *Alfaroa* and *Oreomunna*, which together form a

<sup>1</sup>Manos, P. *et al.* 2001. *Annals of the Missouri Botanical Garden*. 88: 231-269.

<sup>2</sup>Stone, D. 1993. *The Families and Genera of Vascular Plants*. 2: 348-359.



*Engelhardtia*. 1-2, *E. spicata*, Philippines, the distinctive winged fruit and resinous slightly toothed leaves; 3, *E. serrata*, Philippines. (Photographs 1-2, © Ulysses Ferrar; illustration adapted from BLANCO *loc. cit.*)

well supported clade that is distinguished by the opposite leaf arrangement as well as molecular evidence, the derived unwinged fruit of the latter notwithstanding<sup>1</sup>. The addition of *Engelhardtia* also yields a strongly supported clade segregated from the main part of the family that sits within the *Juglans-Carya* alliance. However, the recent contention that *Engelhardtia* is paraphyletic - with *E. roxburghii* sister to the American taxa and segregated as *Alfaroaopsis* - seems to me to lack strong support. The molecular evidence is weak and the morphological distinctions are minor.

The number of Asian species and their morphological variation is poorly understood. The recent revision for the *Tree Flora of Sabah and Sarawak*<sup>3</sup> cites nine species for the genus in Asia, all nine represented in Borneo, but that includes four new Bornean species, three of which are based solely on the type collections. While we might normally defer to the opinion of someone who

has carefully studied all available material, it would seem prudent to avoid the further naming of forms until the biology and genetic structure of local populations is better understood. One can see some ecological parallels between *Engelhardtia* and *Acer laurinum* (Sapindaceae): wind dispersed, putative wind pollination, wide but evidently ancient dispersal with highly localized and distinct populations. The main difference being that *Engelhardtia* is a consistent low density element of the equatorial lowlands while *Acer* is restricted to the mountains.

Dispersal is obviously effected primarily by wind. Pollination in the lowland forests is a mystery since adult trees within the forest are typically hundreds of meters apart. Populations in the mountains are more dense and wind pollination may be effective there. On Mt. Apo, Mindanao, *E. apoensis* is evidently patchily abundant with clustered saplings around the mother trees, the saplings with wavy leaflet margins<sup>4</sup>. On Kinabalu, six species are recorded, at least *E. spicata* and *E. serrata* are common. It is possible that the presence of *Engelhardtia* in the lowlands results from the fortuitous arrival of a seed from nearby mountains. *Engelhardtia chrysolepis* in Hong Kong is nicely illustrated in THROWER *loc. cit.*

## #

### ROSIDS (FABIDS): FAGALES

#### BETULACEAE

**NAME:** From the genus *Betula*, as below. In English as the Birch Family, not Beech, which is the genus *Fagus* in the Fagaceae.

**OVERVIEW:** A monophyletic family of woody plants, comprising six genera and about 150 species of the Northern Hemisphere where they are represented by some of the most well-known and abundant of trees including birches, hornbeams, and alders. They can be described in general as small and medium sized deciduous trees; the leaves simple, alternate with stipules, usually with a doubly serrate margin and pinnate nerves. The flowers and inflorescences are unisexual, the plants monoecious. The fruit is a nut, winged or not, with a single seed.

**CARPINUS.** [Classical Latin name.] About 26 species, especially China, with *Carpinus poilanei* south to Northern Thailand and as far as the Central Highlands of Vietnam (Not illustrated, but see photographs in GARDNER *loc. cit.*)

**BETULA.** [Classical name of the European Birch.] From under 30 species, to over 60, freely hybridizing, with multiple ploidy levels. Especially rich in China with

only *B. alnoides*, occasionally important canopy tree in the very far north of Mainland SE Asia and the Central Highlands of Vietnam at 1700 m. (Not illustrated, but see photographs in GARDNER *loc. cit.*)

**ALNUS.** [Classical Latin name.] About 30 species, especially China, at least *Alnus nepalensis* southward to Northern Thailand and Vietnam, and by the widely cultivated *A. japonica*, used extensively throughout tropical Asia over 1000 m elevation in erosion control and agroforestry.



*Alnus japonica*, cultivated in the mountains of Philippines. (© Leonardo L. Co).

<sup>1</sup>Chen, Z. *et al.* 1999. American Journal of Botany. 86: 1168-1181.

<sup>3</sup>Campbell-Gasis, E. 1995. Tree Flora of Sabah and Sarawak. 1: 233-244.

<sup>4</sup>Seeber, G., *et al.* 1979. Dendrological Characters of Important Forest Trees from Eastern Mindanao. GTZ Eschborn, Germany.

## ROSIDS (FABIDS): FAGALES

## CASUARINACEAE

NAME: From the genus *Casuarina*, as below.

OVERVIEW: The family includes about 95 species divided among four distinct clades as described below, but best treated as a single genus because of their singularity relative to other flowering plants. The family is monophyletic, lies clearly within the Fagales, sister to the Betulaceae<sup>1</sup>, with which they share nitrogen-fixing and wind pollination, but differ so remarkably in form that they held an isolated systematic position until molecular data clarified their ancestry. They differ from other Fagales most obviously in their highly reduced leaves, photosynthetic twigs and in their geographic distribution which is basically Australian with extensions north and east into the Pacific and westward to the Sundaic Region.

CASUARINA. [From the fanciful resemblance of the branchlets to the plumage of the cassowary bird, *Casuarius*.] In Malay as *rhu* and *arbu* with variants in other Malay languages, *agobo* in the Philippines, sometimes as *jemara* or *cemara* in Indonesia.

The genus comprises four monophyletic groups treated in many newer texts as the genera *Allocasuarina*, *Casuarina*, *Ceuthostoma* and *Gymnostoma*. The last is considered sister to the other three and distinguished by exposed stomata in the shallow longitudinal furrows of the branchlets, a basic chromosome number  $x=8$  and the gynoeceum composed of two fertile, biovulate carpels, whereas the other three genera bear invisible stomata in the deep longitudinal furrows of the branchlets, chromosome number  $x=9$  or  $10-14$ , the gynoeceum composed of one fertile and one sterile carpel with a single ovule.

These trees are mostly medium-sized, the leaves reduced to minute teeth in whorls of four to 18 at the joints of the twigs, the photosynthetic function transferred to twigs modified as green switchy needles with pale joints, the internodes of the needle-twigs finely grooved or angled. Rarely aromatic in some of those species segregated as *Allocasuarina*. *Casuarina* trees bear two kinds of twigs differing in their longevity and function. The green switchy needles are the photosynthetic organs, and they live but a short time, perhaps two to three years. The details of their form differ with the individual species, some are short, others long and branched, but they never thicken with secondary growth. These photosynthetic twigs are borne on the stout brown growing twigs that maintain a strong cambial layer and bear vegetative buds in the axil of the bracts from which the new branches develop.

The flowers are unisexual, trees monoecious or dioecious, sometimes switching sexes. Male spikes as slightly modified ends of the ordinary, long needle-twigs: male flowers in whorls, one flower in the axil of each leaf-

tooth and consisting of two minute bracts, one-two minute sepals and one tiny yellowish stamen, always fertile, anthers basifixed; dehiscent via longitudinal slits.

The female-spikes form as the swollen ends of special very short needle-twigs, the flowers in whorls and consisting each of two bracts enveloping a tiny two carpelled ovary with two locules and one style. The two swollen bracts of the female flower form a cavity containing the seed and spread when ripe. The fruit itself is a dry indehiscent nut bearing a single seed with a terminal wing. Gynoeceia of adjoining flowers combine to form a multiple fruit.

The *rhu* trees fix nitrogen through the actions of the root-dwelling actinomycete genus *Frankia*. That symbiosis is obviously a key contributor to the success of the genus allowing rapid growth on the most washed and degraded of soils. The details of the symbiosis are described in a voluminous literature.

The species in Asia are typically more or less gregarious and mostly in open exposed places such that the effectiveness of wind pollination can be presumed. However, when *C. nobilis* grows within peat swamps the role of insect mediation cannot be excluded. Even in dense seaside populations of *C. equisetifolia*, insects are found on the staminate twigs.

Dispersal of the small winged seeds in tropical Asia is also by wind. The great diversity of species in Australia include a broader range of dispersal types.

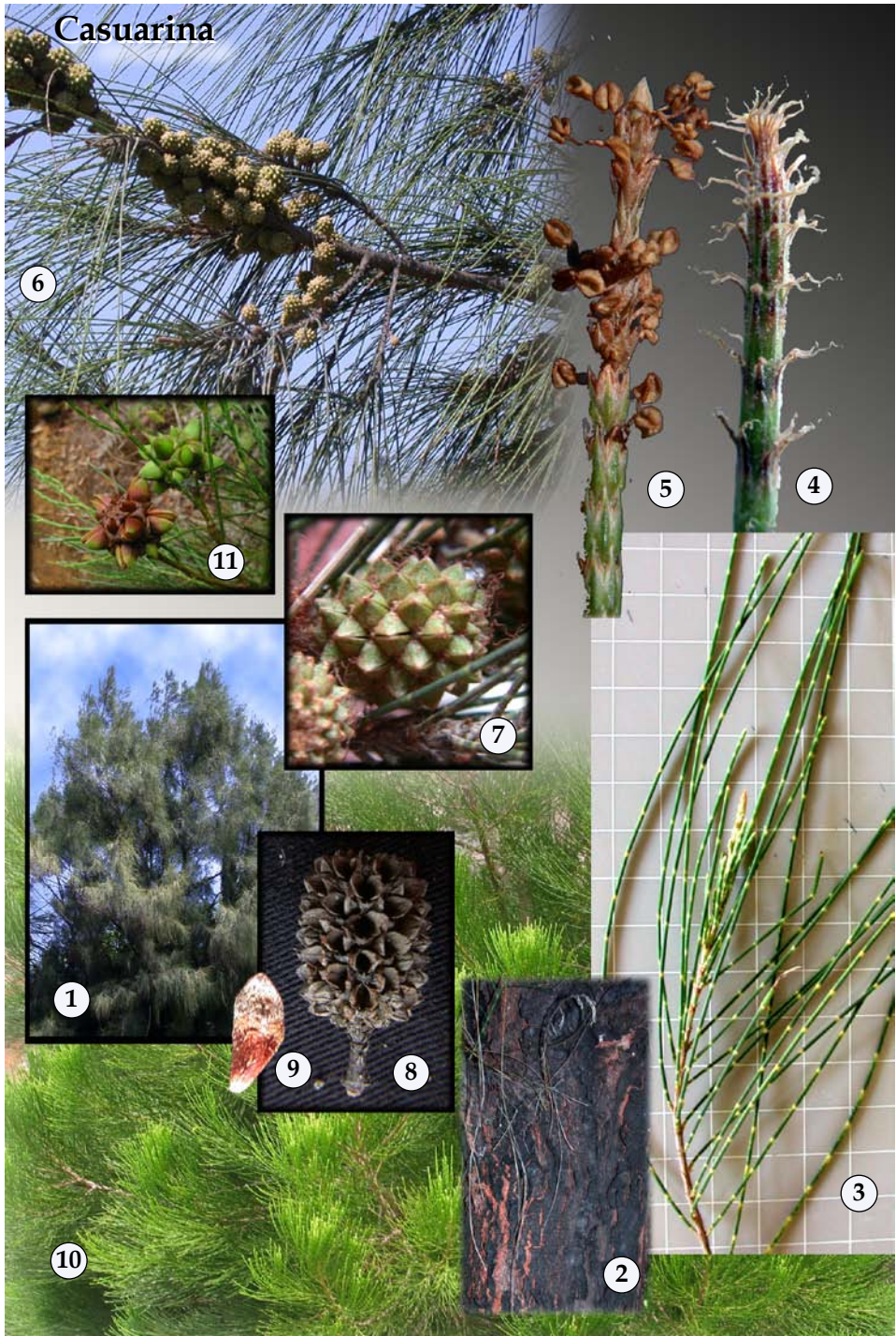
The most widespread and obvious species is *C. equisetifolia*, the sea-side *rhu* tree found along most sandy and rocky shores from Australia to the Pacific Islands and east to the Bay of Bengal. Otherwise we have a set of related species in the alternative genus *Gymnostoma*, all roughly similar but differing in some details of form and especially in ecology: *C. rumphiana* from lower mountains in Ambon, Sulawesi, and scattered as far north as Philippine Islands; the more abundant *C. sumatrana* of mountains in Sumatra and Borneo (and cultivated with increasing frequency); *C. nobilis* is a locally dominant tree of Bornean kerangas, peat swamps, land slips and ultra-basic outcrops; *C. junghuhniana* is native to the highlands in Indonesia where it can form pure stands on the volcanic slopes above 1500 m. A putative hybrid between this species and *C. equisetifolia* is commercially cultivated in Thailand.

I might also mention the introduced *C. glauca* which is increasingly planted for reforestation despite the problems caused by *C. equisetifolia* as an invasive in Florida and Hawaii.



<sup>1</sup>Sogo, A. *et al.* 2001. Journal Journal of Plant Research. 114: 459-464.





*Casuarina*. 1-9, *C. equisetifolia*, Philippines; 1, open multi-branched crown; 2, bark; 3, twig with lateral branches; 4, photosynthetic twig tip, whorls of scale leaves; 5, exerted anthers from scale leaf axils; 6, pistillate tree with clusters of cones; 7, unripened cone; 8, old dry cone with spreading fruit, 2 cm long; 9, winged seed, 4 mm long; 10-11, *C. sumatrana*, Philippines; 10, dense green branches; 11, pistillate cone.